TEMPORAL SEGREGATION OF HUMPBACK WHALES DURING MIGRATION IN SOUTHERN HEMISPHERE WATERS *

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All available data on post-war catches and some pre-war catches of humpback whales in the southern hemisphere between 66°S and 1°S have been examined for evidence that some age or reproductive categories migrate north, and south early in the season, while others follow in sequence later. The categories that showed significantly different time sequences between groups in non-polar waters were as follows:- all immature humpbacks (no significant difference between males and females), mature males (regardless of size), and mature females subdivided according to reproductive stage as pregnant, lactating or resting. Based on the average intervals between the mean dates for each category at whaling localities between 41°S (Cook Strait, New Zealand) and 1°S (Congo), lactating females accompanied by weaning 'yearlings' migrate north earliest and are followed by immature humpbacks, mature males, together with resting females and finally pregnant females at 12, 20, 23 & 31 days later respectively. During the return migration southwards, mixed females (including those in early pregnancy) occur first together with immature whales, and are followed by mature males and females in early lactation 10 and 16 days later. Reasons for believing these time intervals to be minimal are discussed. In general, humpbacks appear to return south in the same order in which they travelled north, but some females change status so that those that travel north early when near the end of lactation, may return south early as pregnant animals. Others that travel north late as pregnant animals, return south late as cows accompanied by young calves. Mature females, when pregnant, appear to spend a prolonged period in Antarctic waters but when suckling a calf they spend a substantially reduced interval in cold waters. Antarctic catches appear to have been taken over too short a season to demonstrate sequences during the entry and exit of humpbacks to Antarctic waters.

Humpback, Megaptera, southern hemisphere, migration, segregation.

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The published information on the main features of humpback whale migrations between warm water breeding regions and cold water feeding regions have been described and reviewed by a number of workers. These are referred to by Dawbin (1966), so the present account will be confined to a discussion of segregation during the migratory cycle of humpbacks.

Ever since the International Whaling Statistics began publishing tables which classified the sex and sizes of whales caught in all main whaling grounds, it has been clear that there is a marked disparity in the composition of humpback catches from Antarctic regions as compared with those from temperate and tropical regions. While females usually predominate in Antarctic catches, males tend to predominate in catches from warmer waters. This change of composition suggests that the humpback population does not remain homogeneous throughout the season, but undergoes some degree of segregation into sex

and possibly age groups at certain phases of its seasonal movements. Mackintosh (1942) has discussed evidence of changes in the composition of humpback catches (inter alia) during the Antarctic season, but accounts of sequential changes in composition in other southern hemisphere regions have tended to describe movements in rather localised areas.

Segregation between whale categories may occur in space (geographical segregation) or in time. Geographical segregation is here regarded as the entry of one sex, age or other specified class within a species, to an area which is not entered by other classes of that species. The classes are then clearly separated in space. In time segregation, one or more classes enter an area at an earlier date than the other classes, but the latter enter the same area at a later date. At any one moment the classes may be separated in space but they all pass through the same area although at different times.

^{*} This work was completed in 1963, the year in which the International Whaling Commission banned the taking of southern hemisphere humpback whales.

Sperm whales provide an excellent example of geographical segregation. Mature males only are found at high latitudes while females and immature animals do not occur south of about 45°S. There are differences in sex ratios and in the proportion of mature and immature humpbacks represented in catches at different latitudes, but there are no known cases of such marked geographical segregation between categories of humpbacks as occurs with sperm whales. However, at many localities there are regular differences in the catch composition with change in season.

It is suggested that many of these cases may be the result of some humpback categories migrating to warm waters early in the season while others tavel at varying intervals later. Any such tendency would change the relative proportions of those remaining after the start of migration as well as cause sequential changes in the composition of the stock migrating past any fixed point.

The object of the present study is to identify the reproductive stage of each humpback and relate this to the arrival time of each animal at specified latitudes during the migratory cycle. It is an attempt to specify the reproductive or age categories that tend to migrate earliest in the season and to determine the time interval between that of their peak density and that of categories which migrate at a later date. As part of time segregation, the order in which specified categories travel and the mean interval between categories is referred to in this account as 'time sequence'. It is this as distinct from geographical segregation that is the main subject of the present study.

MATERIAL AND METHODS

With the exception of sighting records on cows accompanied by calves, humpbacks cannot be classified accurately into size, sex, or reproductive stage categories by observations at sea. Catch data on animals processed at whaling stations or factory ships have been published regularly in International Whaling Statistics, but the data are grouped into monthly categories or into size categories unrelated to dates. The object of the present study has therefore necessitated an analysis of the available data on individual humpbacks for those cases that specify the length, sex, stage of pregnancy, geographical position and date of catch.

MATERIAL EXAMINED. Data have been obtained for each of 65,600 humpbacks caught in the southern hemisphere. Of these 38,100 were caught in post-war

years and 27,500 were caught in pre-war years. Both samples include catches from Antarctic through to equatorial waters.

From temperate and tropical waters the post-war data relate to 28,243 humpbacks as follows:- Cook Strait, New Zealand 1922; Great Barrier Island, New Zealand 264; Tonga 84; (data and gonads collected by the writer and field collaborators); Albany, West Australia 699; Carnarvon, West Australia 5889; Point Cloates, West Australia 3321; Byron Bay, New South Wales 1040; Moreton Island, Queensland 6206; Norfolk Island 880; Durban, Natal 854; Madagasear, pelagie 2014; Congo 4071; (data provided on microfilm by Mr E. Vangstein, Sandefjord with the permission of the managers of the respective whaling companies. Valuable supplementary data on Australian catches was provided by Dr R.G. Chittleborough). Pre-war data includes 14,515 humpbacks as follows:- Coast of Natal 2621; Madagascar 1223; Western Australia land station 3426; Western Australia, pelagic 7244. Professor J.T. Ruud provided the pre-war records together with summarising tables and graphs prepared by himself and collaborators.

Antarctic catches in post-war years include 9857 humpbacks taken in late December and early February. In the 1932/33 to 1938/39 seasons, catching in Antarctic waters occurred from early November to late March, and data on 12,985 humpbacks caught between 65°S and 66°S have been obtained from Mr E. Vangstein who provided duplicate I.B.M. cards for each animal. Shore whaling in subantarctic waters has, in recent years, been confined to South Georgia where humpbacks have formed a negligible part of the catch. There were substantial eatches earlier from South Georgia and other coastal waters of the Falkland Islands Dependencies and records exist for those caught between 1910 and 1917. These data are lodged in the British Museum (Nat. Hist.) where Dr F.C. Fraser kindly allowed me to examine them. South American humpback catches have been small and secondary to those of other species, so they have not been included in the present study.

METHODS. Gonads and other material and data obtained in New Zealand and Tonga were sufficient to classify the local catches in a number of ways that could be tested for statistically significant differences. Subdivisions into sex, and size categories showed little difference in the date of peak density of small males compared with small females, but there were substantial and inconsistent differences between the dates of peak density of large males as compared with large females. Classification based on reproductive data showed little or no difference between the time sequence of immature males and immature females, but suggested that the timing of mature females could be related more closely to their stage of breeding than to their size. Females at the end of lactation, resting females and pregnant animals followed different time sequences of which that followed by resting females was most similar to the time sequence of mature males (Dawbin, 1960).

Except for the specified pregnant females, data on the reproductive condition of humpbacks are listed rarely in catch returns. In New Zealand catches the ovaries from 611 females and testes weights of 630 males indicated that females became mature at 39'6" and males at 38'. Those from which gonads had not been obtained were therefore classified as mature or immature according to whether they were above or below these lengths. Mature females whose mammary glands gave evidence of recent activity and those recorded as accompanied by a 'yearling' were classified as being at the end of lactation. Pregnant females are easy to recognize during processing as the foetuses of northbound humpbacks are large at New Zealand latitudes. The remaining mature females include resting animals and almost certainly include some that were at the end of lactation but for which there is inadequate data to allocate them to this category.

From the large Australian catches, Chittleborough (1958) has examined numerous gonads and found a close correlation between length and state of maturity using 36'9" as mean length for maturation of males and 38'6" as mean length for females. These lengths have therefore been used in this study to classify Australian catches and in view of the large samples on which the criteria are based, they have also been applied to data from all regions beyond Australasia. Because of the slight discrepancy between the estimated maturation lengths in Australia and New Zealand, data from other regions have also been analysed on the New Zealand criteria and by arbitrarily varying the lengths from 37 to 39 feet for males and 38 to 40 feet for females. The results did not produce significant changes in the calculated time sequences so the original criteria on maturity have been retained in the present analysis.

Some separation of mature non-pregnant females into stages of lactation or resting has been possible only for certain Australian catches. Dr Chittleborough has kindly provided data from four seasons' catches in Western Australia relating the proportion of mature females whose mammary glands showed signs of recent activity to that of other non-pregnant mature females. The pre-war Western Australia catches made before the minimum size length of 35 feet was established, include many whales whose length indicates that they were almost certainly yearlings travelling with mothers near or at the end of lactation. In other regions non-pregnant mature females have been classified as a mixed group including resting and unspecified animals (shown as R & U in tables) of which an unknown proportion would be in late lactation.

With the above reservations, eatch data on each humpback was used to classify the animal as immature (male or female); mature male; lactating, resting, pregnant or unspecified mature female.

Catches from relatively fixed positions (land stations or coastal factory ships) were classified as above and then grouped for each category into weeks for each season. As differences between time sequences per season at any one locality proved non-significant, the data for successive seasons were pooled for each week as shown in the appended tables.

The weeks were specified starting from 1st May which is the earliest commencing date for the most southern shore station under consideration (Cook Strait, 41°S). To facilitate comparable analyses for each station, the weeks were arbitrarily numbered commencing from May 1 and the same week code system has been used for all non-polar whaling localities, i.e., May 1-7, May 8-12; May 15-21, 3; etc. The numbering for Antarctic catches commences with November 6-12, 1; etc.

From the weekly frequencies of each humpback category per locality, the mean date, standard deviation and 95% confidence limits of the mean were calculated. The limits used were two standard errors on either side of the mean for samples exceeding 30 and Yates correction in the few cases where samples have been smaller than The results have been presented in the graphical form (with slight modifications) described by Hubbs and Hubbs (1953). In the present graphs (Figs 23 & 25) the mean date is indicated by a white line within the black area that represents the 95% confidence limits on either side. Range has been omitted since this is determined frequently by a lone early or late whale and is therefore not relevant to the main theme of this study.

As pointed out by Hubbs & Hubbs, considerable reliance can be placed on the significance of the difference between samples, if the corresponding rectangles (referring to the total range of four standard errors of the mean) are only slightly separated, or if the overlap is not more than about 33% of the length of the shorter of the two rectangles. An approximate idea of the significance of an observed difference can be ob-

tained by inspection of Fig. 4 in Hubbs and Hubbs. In all doubtful cases, t tests were applied to determine whether or not a difference was significant at the 5% level or less. Coded means have been reconverted to calendar dates in Tables 12, 14 & 19.

Antarctic pelagic catches have been subdivided firstly into groups according to latitude and secondly into sectors of longitude subdivided into latitudes before classification as above.

While the tables list the humpback groupings used in the analyses, the graphs for clarity show fortnightly groupings to avoid some of the weekly random fluctuations or the alternative of smoothing the data. Graphs of percentage composition per fortnight are included as a guide to the probable composition of catches concentrated into selected portions of the humpback season and as a comparison with earlier data which have been published in the form of percentage changes during the whaling season. It must be emphasised that such data are of very doubtful value if applied to the season as a whole. For example, Fig. 2 suggests a fairly continuous replacement of immature humpbacks by mature animals throughout the season, but Fig. 1 shows that this is the result of a relatively small time difference in the periods of peak density of immature compared with mature whales. Other figures illustrate many comparable cases,

The separation of northbound from southbound humpbacks has, in the absence of individual data on direction of travel, depended on sighting records of the proportion of all humpbacks travelling north or south during the migratory season. Sources of error in such data are discussed below. Sampling Error. Catches are not completely random samples of the populations from which they are drawn, and the main sources of sampling error are considered below.

a) Size. The minimum length of 35 feet specified by the International Whaling Commission in 1937 normally gives complete protection to the 'yearling' group that range from about 28 to 31 feet in length. Data on yearlings must therefore be obtained from catches made prior to 1937 or from sightings at sea. Members of this group are seen very frequently accompanying their mothers in higher temperate latitudes, but they usually become independent in the tropics.

A proportion of immature whales of other age groups included in the 30 to 35 feet length range, are also protected by the size regulation, but those between 35 feet and the size of sexual maturity can be caught. However, they are likely to be

under-represented due to gunner selection for whales of greater size. The degree to which this occurs has varied between stations and seasons due to changes in relative availability of larger whales, and the effects in some cases of operating under quotas. Within the group of immature whales which are caught, there is no known means of distinguishing the sexes at sea, so, as females reach a greater size than males before becoming sexually mature, they would be expected to form a higher proportion in the catch of immature whales than that in which they occur in the whole migrating population of immature whales.

Mature females grow to a greater maximum size than mature males and gunner selection for the largest whales would be expected to increase the relative representation of this group in the catch compared with the population as a whole. However, this effect is counterbalanced to varying degress by the next factor.

 b) Presence of Calves. Cows accompanied by suckling calves are given protection by the International Whaling regulations, and this protection is of greatest importance among southbound humpbacks returning from the breeding grounds, and among those in the Antarctic feeding grounds where the calves are still suckling. It is less important in the temperate zones where northbound calves are in the process of being weaned and are almost certainly capable of continuing their existence independently of the mother, so the mother is often hunted. However, some whalers have actively avoided the mothers of these weaning yearlings, and the difference in policy relative to this group has provided some marked differences in catch composition between stations.

 c) Pregnant Whales, It is generally assumed that pregnant females cannot be identified as such at sea and no regulations relating to this class of whales have been made. However, the proportion of pregnant whales changes during the northward. migration because of the birth of calves at various latitudes en route. Towards the end of northward movement a high proportion of females which were in late pregnancy when they left the Antarctic seas, have undergone partutition becoming recognizable as cows accompanied by young calves and they then receive full protection. By the time the southward migration commences all whales which had left the Antarctic in late pregnancy have delivered calves and, except for those which have lost their calves, this whole group is protected during their return migration and subsequent stay in Antarctic waters.

There is some evidence of an additional complicating factor in certain regions where whales close to partutition are encountered. At least one gunner (the Master gunner at Norfolk Island) has stated that he can recognize females in very late pregnancy by their slower movements and general behaviour, and he is therefore able to select against such animals. The lack of females in late pregnancy in Norfolk Island catches at periods when this group would be expected to pass the island, lends some support to his contention.

Another group of pregnant whales are those which are southbound shortly after conception in the tropics and consequently the foetuses are very small during the southward migration. There are relatively few tropical and temperate zone records of this group partly because the greater part of southern hemisphere shore whaling is concentrated on northbound animals and partly because the very early foetuses are difficult to find in the brief examination which is all that is possible at many shore stations.

d) Curtailment of Season. Catches in some regions have been restricted to limited parts of the humpback season by specifying dates between which catching is permitted or by imposing quotas which, when filled, close the season. Antarctic catches since 1949 have been made in periods ranging from four to fourteen days in any one season, so have been too short to demonstrate time sequences within a season. There is even some evidence that the three of four month catching periods between 1931 and 1939 were probably insufficient to sample adequately the sequence of humpbacks during arrival and departure from the feeding grounds.

Quotas setting the upper limit of catch were applied to all Australian whaling stations during post-war years. When humpbacks were abundant, the existence of quotas encouraged companies to delay whaling until there had been numcrous sightings that would assure the gunners of regular catches with good opportunities of selecting large animals. The earliest humpbacks were therefore under-represented in catches. When quotas were filled quickly the late humpbacks were not sampled. In some cases catches sampled part only of the northbound stock and in other seasons part of the southbound as well as all but the earliest northbound whales were sampled.

e) Specification of northbound and southbound humpbacks. At whaling localities north of 30°S, there is some overlap between the last northbound humpbacks and the earliest southbound humpbacks, but the catch data do not specify the

direction followed by individuals caught. Fortunately there is some information giving the approximate dates on which equal proportions of humpbacks are sighted travelling north compared with others travelling south past each locality except Congo. The latter, however, is probably close to the tropical end point of migration of the local humpbacks. All humpbacks caught prior to the date on which equal proportions travel north and south are classified as northbound and those after it are classified as southbound. Some of the humpbacks that travel north late and some of those that travel south early are therefore allocated incorrectly.

f) Effects of Sampling Errors. The sampling errors due to size selection, protection of cows accompanied by calves and the changing proportions of pregnant animals during migration, change substantially the degree of representation of several humpback categories at various latitudes, but there is no evidence that it modifies significantly the mean dates calculated for the categories specified in this study. So long as the type of selection at any one station remains fairly constant throughout the season, the degree of under- or over-representation of each category should also remain relatively steady throughout the season. The effect of under-representation is a tendency to increase slightly the standard error of the mean rather than the position of the mean. Providing each category is homogeneous and represented by numbers adequate for analysis, catch samples appear to be a satisfactory guide to the time of migration past each locality.

The apparent migration times of heterogeneous groups are, however, changed whenever there is a difference in selection between groups contained within the complex. Catches of mature females for example can rarely, if ever, be subdivided completely into lactating, resting and pregnant categories. There is frequently a heterogeneous group which includes resting and an unknown but probably variable proportion of unspecified animals (R & U group in tables), that are selected differently within a single locality. Among northbound whales, R & U includes females near or at the end of lactation, resting females and negligible number of unrecognized pregnant animals.

Even at stations where the data and material allow classification of most mature females into lactating, resting or pregnant, it is reasonably certain that some recently lactating animals are unrecognized as such and are classified as resting. As lactating or recently lactating animals tend to

travel northwards earlier than other categories, the merging of some of these with resting animals displaces the apparent mean date forwards by an unknown amount. However, the displacement is presumably greatest when no separation of lactating and resting animals is possible, and least when a high proportion of lactating animals can be specified separately from resting females. This is further complicated by changes in status of some mature females with latitude and with the differences in gunner selection referred to in section (b) above. To indicate this diagrammatically in Fig. 23, confidence limits have been omitted in the case of mixed females, but calculated means and standard deviations are included to account for all specimens. The actual values obtained are retained for reference in Table 12. Values for those 'resting' females from which a high proportion of lactating animals could be separated are shown in Fig. 23, but the above reservations on the relative homogeneity of this group should be borne in mind.

The mixture of all categories of mature females in contrast to mature males has been used frequently in past comparisons and has been shown in Figs 1-22 as a dotted line. These figures suggest great variability in seasonal trends between localities, but examination of data on the subdivisions within all mature females shows that this apparent variability is largely the result of changes in the relative proportions of the subdivisions.

Among southbound mature females there is a mixed group that includes resting females and some in early pregnancy, but there is no evidence that gunner selection operates differently between the two categories at any one locality or between different localities. As the available data are insufficient to separate these categories, estimated values for the mixed group are included in Fig. 25 as well as Table 14, but the group is clearly not as homogeneous as any of the other south-bound categories specified.

Any curtailment of season that delays catching until after some of the early humpbacks have passed the catching zone results in a calculated mean date that is late compared with mean date which would have been obtained if the early animals had been represented in the catch. Similarly, if the season ends before the last category of humpbacks has passed, the calculated mean date for the latter will be displaced forwards. Both early and late curtailment of the season therefore causes displacement towards the general mean of the total catch. Incorrect allocation of some individuals into northbound or south-

bound categories in cases of overlap between the two migrating streams also tends to minimize calculated differences between the timing of categories. Differences that nevertheless prove highly significant are likely to be real and to be greater than indicated in this study.

RESULTS

The time sequence followed by specified categories of humpbacks as they travel to and from tropical breeding regions has been studied from samples obtained at a range of latitudes. Those in temperate and tropical waters have been considered first followed by an examination of those in Antarctic latitudes. The samples from temperate and tropical regions show no difference in trends between separate breeding stocks off west Africa, east Africa, west Australia and east of Australia so the coastal whaling localities have been considered in order of latitude from south to north (except for Tonga) regardless of longitude. This arrangement approximates the sequences in which lines of latitude are traversed by northbound humpbacks. These form the largest proportion of the catch sample at all temperate and tropical latitudes except at Tonga where southbound humpbacks only are caught. Catch samples from the latter have threfore been discussed after a consideration of those from other nonpolar localities, followed by the results obtained from Antarctic waters.

TEMPERATE AND TROPICAL WATERS

Cook Strait, New Zealand, 41°S. It has been shown previously (Dawbin, 1956) that catches in Cook Strait are taken almost exclusively from whales during one stage of migration, i.e. northbound towards the breeding areas. Southbound humpbacks pass through Cook Strait exceedingly rarely. Lookouts are posted at high vantage points some weeks before the humpbacks are expected to traverse Cook Strait, and catching commences immediately after the first few humpbacks have been seen. Operations continue until a week or more has passed without sighting a humpback. The catch, therefore, includes samples from start to end of the northward migration past Cook Strait, and the majority of those sighted have been caught.

The small hoat catching methods and the days lost through bad weather ensures that gunners catch whales primarily through availability with little possibility of selection, except for rejection of the smallest whales.

	Lam	ature			Ma	true		
Staff of week	60	0+	Allimmstures	*0	Lacı. 9	R+U \$	Preg. 9	All humpbacks
1/5		1	1					1
8/5	3	5	8		2			10
15/5	ь	6	12	5	5	1		23
22/5	24	28	52	23	25	3		103
29/5	68	47	115	-31	21	13	2	182
5/6	55	53	108	74	27	1.0	4	227
12/6	53	42	95	9.4	22	3.3	4	252
19/6	49	31	80	134	8	28	20	270
26/6	37	31	68	123	4	23	29	247
5/7	23	16	39	Lūn	.5	32	24	200
10/7	-6	7	15	7.5	1	17	28	136
17/7	2	8	10	53		19	22	104
24/7	3	-8	11	46		21	12	90
31/7	5	ŧ	6	22		5	10	43
7/8				ġ		3	4	16
14/8				7		4)	12
Total	336	284	620	802	120	216	164	1922

TABLE 1. Weekly catches of specified humpbacks, 1947-1960. Cook Strait, NZ, 41°S.

Samples have been obtained through the catches of each of the seasons 1947 to 1960 totalling 1922 humpbacks. This is supplemented by sighting data on others, including the highly significant group of weaning yearlings observed as accompanying their mothers.

Females in late lactation form the earliest category at Cook Strait (Figs 1-2, Table 1). Most have been eaught before mid-June, and none later than mid-July in any of 14 seasons. During this period the size of the local humpback stock appears to have been fairly stable, so the number of females in late lactation (as defined above) should have been approximately the same as those in late pregnancy, except for a slight reduction caused by the natural mortality of some calves before weaning. The 120 recorded compares with 164 in late pregnancy, and suggests that a few in late lactation may have been unrecognised and grouped among the 216 recorded as resting and unspecified. However, no 'yearlings' accompanying their mothers have been observed after mid-July, so it seems probable that the time sequence indicated by the recorded females in late lactation is substantially correct.

Immature males and Iemales (Table 1) show no significant difference in mean dates. They have

therefore been combined in Figs 1 and 2 which shows the number and percentage frequency per fortnight respectively. It is evident that largest numbers occur about one week later than late lactating females, and about two weeks earlier than those of mature males. Immature animals have been represented from the beginning of each season, but none have been caught during the final two weeks in any season. Percentage Irequences (Fig. 2) show that immature animals form a steadily decreasing proportion of the catch per fortnight as the season progresses, but Fig. 1 shows that this is the result of a relatively small time difference between the attainment of peak density by immature animals compared with the categories of mature humpbacks.

Mature males form the largest single category of humpbacks at Cook Strait. None have been caught before mid-May, but the group has been represented during the remainder of the season. Peak density occurs in late June with a mean date of June 29.

Resting females, including a few unspecified animals that may have been in late lactation, have followed a very similar time sequence to that of mature males. There is no significant difference in mean dates or duration of season between these categories, but there have been nearly four times as many mature males as resting females in the eatch.

Females in late pregnancy have formed the last category in all seasons during which they have been represented. None have occurred in May and the mean date (July 8) is about one week later than those of mature males or resting females. Pregnant Temales are therefore approximately one month later than those in late lactation.

Great Barrier Is., New Zealand 36°S. As at Cook Strait, the humpback catches from waters near Great Barrier Island include a high proportion of all those sighted, and represent all categories except those of smallest sizes. The last northbound humpbacks leave the area some live or six weeks before the return of the earliest southbound animals, so there is no difficulty in separating animals on direction of travel. Data with gonads and other material have been obtained during the three seasons 1959-1961 relating to 231 northbound and 33 southbound animals, but the material does not include mammary gland samples or observations on yearlings accompanying their mothers. It is therefore impossible to specify lemales in late lactation.

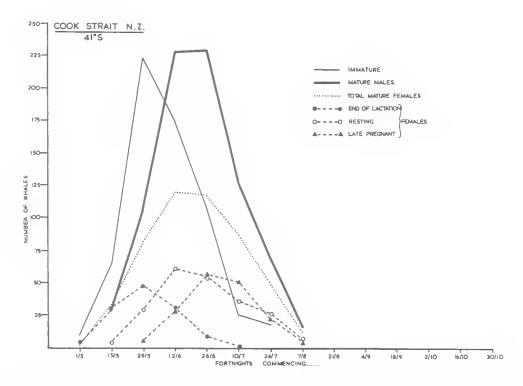


FIG. 1. Fortnightly catches of specified humpback categories, 1947-1960. Cook Strait, NZ, 41°S.

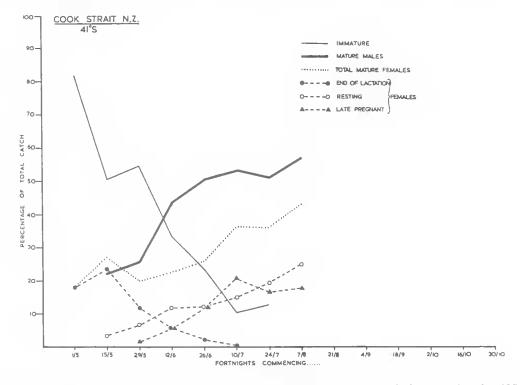


FIG. 2. Fortnightly percentages of specified humpback categories, 1947-1960. Cook Strait, NZ, 41°S.

TABLE 2. Weekly catches of specified humpbacks, 1959-1961. Great Barrier Island, NZ, 36°S.

Immature Mature All humpbacks immatures Start of week \supset Preg. Lact K+ Alli 22/5 29/5 Q 5/6 12/6 19/6 26/6 3/7 10/7 17/7 24/7 31/7 7/8 14/8 21/8 28/8 4/9 11/9 18/9 25/9 2/10 9/10 16/10 23/10 30/10 Total

The earliest identifiable category comprises the immature animals (Figs 3-4, Table 2) which are represented in catches from the start of the season in late May until about mid-July, but none have been caught in the last two weeks of the northbound season. The mean date is 11 days earlier than that for mature males.

Mixed mature females include both resting and unspecified lactating females, and are represented throughout the season. The estimated mean date is mid-way between those for immature animals and mature males, so is relatively earlier than resting females at Cook Strait. This is almost certainly the result of including all the late lactating females, since this group elsewhere tends to travel earlier than other mature females.

Mature males form the largest group and are represented throughout the season. The mean date is 11 days after that of immature animals, and

TABLE 3. Weekly catches of specified humpbacks, 1952-1958. Albany, WA, 35°S.

	Imm	ature			Ma	ture		
Start of week	ю	0+	All immatures	60	Lact. 9	R+U \$	Preg. 9	All humpbacks
29/5	1	0	1	1	2	- 1	0	4
5/6	2	6	8	1	6	1	0	16
12/6	8	10	18	7	16	2	0	43
19/6	10	-11	21	19	10	6	0	56
26/6	13	8	21	36	8	5	0	70
3/7	14	17	31	39	8	-11	6	95
10/7	17	9	26	46	9	19	4	104
17/7	9	4	13	48	5	20	. 7	93
24/7	5	9	14	33	3	17	14	81
31/7	3	1	4	29	2	17	13	65
7/8	1	2	3	11		5	12	31
14/8	2	1	3	10		5	7	25
21/8	0	0	0	6		3	1	10
28/8	0	1	1	3		1	1	6
Total	85	79	164	289	69	112	65	699

8 days earlier than for pregnant females. Pregnant females form a small sample, but all were obtained after the first month of whaling, and the group was clearly the last northbound category.

Southbound humpbacks caught between mid-September and late October form a small sample in which there is no demonstrable difference in timing between mixed females and immature humpbacks, but the five mature males obtained were all caught after mid-October. (Fig. 25, Tables 2, 14).

Albany, WA, 35°S. The catch is taken from an exclusively northbound population, as hump-backs returning south from Western Australian coastal breeding areas follow a route some distance west of Albany. Although quotas have been applied in each season, catching has been carried on throughout most of the local humpback season before the quotas were filled. Except for protection of undersized whales, the Albany catch appears to be a representative sample of the local stock throughout its season of migration past the locality. Catching has commenced about three weeks later than at the higher latitude of Cook Strait. Catches in the seven seasons 1952-1958 include 699 humpbacks.

Females classified as at or recently in late lactation form the earliest category (Figs 5, 6, 23, Tables 3 and 14) with peak density in mid-June

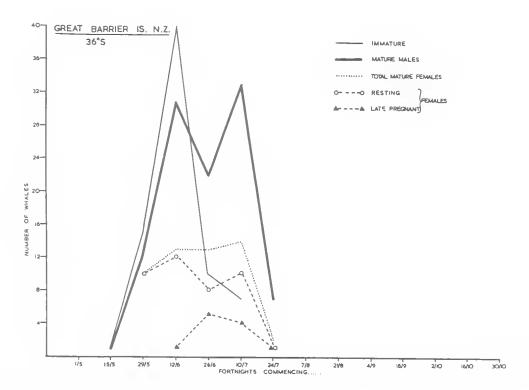


FIG. 3. Fortnightly catches of specified humpback categories, 1959-1961. Great Barrier Is., NZ, 36°S.

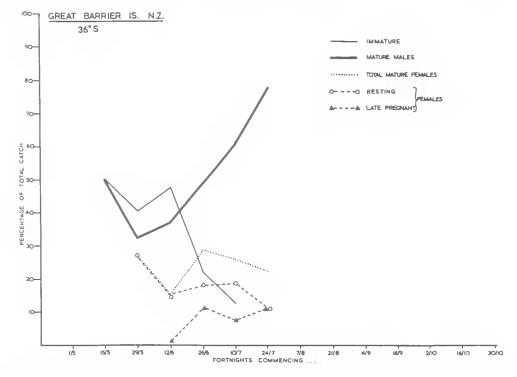


FIG. 4. Fortnightly percentages of specified humpback categories, 1959-1961. Great Barrier Is., NZ, 36°S.

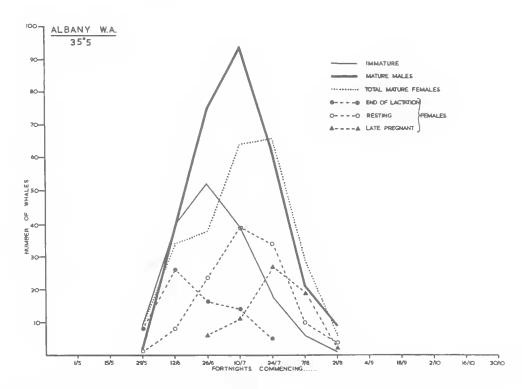


FIG. 5. Fortnightly catches of specified humpback categories, 1952-1958. Albany, WA, 35°S.

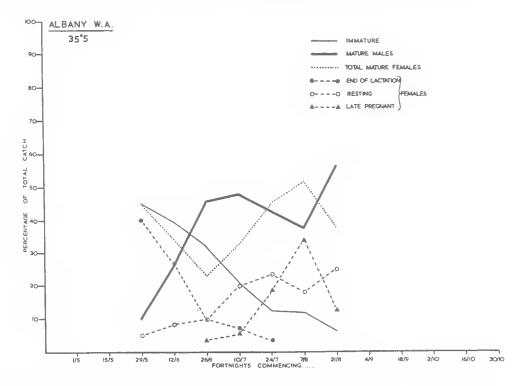


FIG. 6. Fortnightly percentages of specified humpback categories, 1952-1958. Albany, WA, 35°S.

TABLE 4. Weekly catches of specified humpbacks, 1948-1954. Durban, Natal, 30°S.

	Imm	ature			Mai	ure		
Start of week	40	C.	All immatures	*⊙	Lact. 9	R+U \$	Preg. 9	All humpbacks
15/5	0	1	1	0		0		1
22/5	2	0	2	0	- 2	0		2
29/5	5	2	7	1		1		9
5/6	3	5	8	6		6		20
12/6	10	13	23	10		4		37
19/6	21	17	38	20		12		70
26/6	28	37	65	31		1.5		111
3/7	22	24	46	42		15		103
10/7	18	20	38	37		15		90
17/7	14	23	37	24		21		82
24/7	14	16	30	29	y ()	16		75
31/7	7	12	19	6	L 10	10		35
7/8	7	6	13	4		5		22
14/8	2	3	5	2		3		10
21/8	6	8	14	6		4		24
28/8	2	10	12	2		2		16
4/9	0	0	0	2		1		3
11/9	3	2	5	5		5		15
18/9	11	12	23	13		10		46
25/9	12	12	24	19		7		50
2/10	1	5	6	7		6		19
9/10	3	1	4	4		3		11
16/10	0	0	0	1		0		1
23/10	0	0	0	1		0		1
TOMO	0	100	0.4	1		0		1
Total	191	229	420	273		161		854

and none during the last four weeks of the season. The mean date (June 28) is about one week earlier than that of immature whales. The latter are represented throughout the season, but of 164 caught, seven only were caught during the last four weeks of the season. Mature males have also been caught through the season, but peak density occurred during July and the mean date was 10 days later than for immature whales. Resting and unspecified females had a time sequence similar to that of mature males. The small difference in mean dates is not significant.

Females in late pregnancy have not been recorded during the first five weeks of the season, and their mean date is about two weeks later than that of mature males. They have occurred one month later than late lactating females, and they

comprise the last category to migrate northwards past Albany.

Durban, Natal 30°S. Humpback catches from Durban during post-war years have differed from those made near any of the other temperate and tropical localities under consideration in being secondary to catches of other species. Sperm and fin whales have formed the major part of the catch, and both of these species tend to occur at a greater distance from shore than most humpbacks. While the writer has no personal knowledge of the local conditions, the total catch composition suggests that humpbacks are caught as opportunity arises between catches of the more valuable and intensively sought sperm and fin whales, so the humpback catch is possibly not a consistent sample of the locally migrating stock.

The composition of humpback catches is unusual in the very high proportion of immature animals, which on the present criteria represent nearly half the total catch, and on the criteria used in International Whaling Statistics they form about two thirds of the total catch. The absence of foetus records suggests that pregnant females traverse waters closer to shore or further out to sea than the main catching zone, or that the data on pregnant females is incomplete. The overall low percentage of mature females shows that incomplete recording cannot be the full explanation, and may not even be part explanation.

The writer has no substantial data on which to scparate northbound from southbound animals, but the bimodal peaks in the present and Matthews (1937) data indicate that the change occurs during August. Trial analyses were carried out on data from the start of season to August 13, August 20, August 27 and September 3, with little difference in sequence resulting. Mid-August (actually up to August 13) has been used in the calculations shown in Table 12 & Fig. 23. The post-war data relates to 854 humpbacks caught during the 1948-1954 seasons, and includes 667 which have been classified as northbound.

Immature whales form the earliest identifiable category, followed by mature males, then mixed females, but the time intervals between the mean dates of these categories (Table 12) are too small to be significant at the 5% level.

Pre-war catches generally included a higher proportion of humpbacks than other species, so they are likely to be a more representative sample of the local humpback stock. Catches by one company at Durban in 1934 and 1935 included 547 that have been classified as northbound since

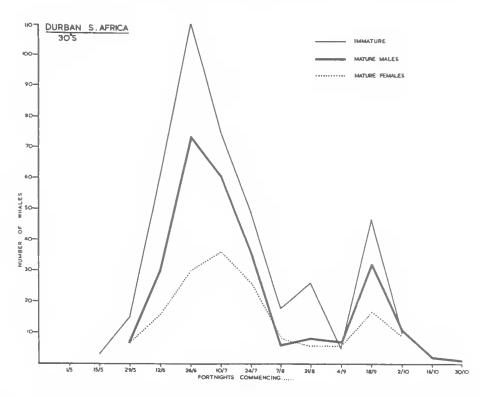


FIG. 7. Fortnightly catches of specified humpback categories, 1948-1954. Durban, Natal, 30°S.

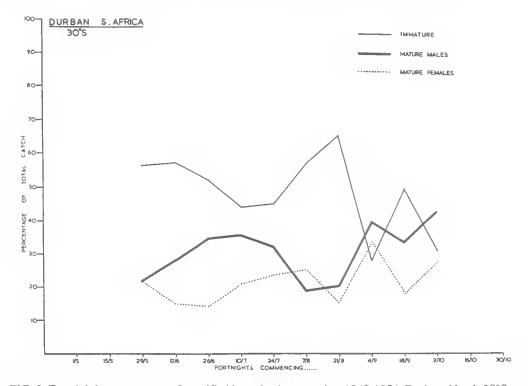


FIG. 8. Fortnightly percentages of specified humpback categories, 1948-1954. Durban, Natal, 30°S.

TABLE 5. Weekly catches of specified humpbacks, 1954-1961. Byron Bay, E Australia, 29°S.

TABLE 6. Weekly catches of specified humpbacks, 1956-1961. Norfolk Island, 29°S.

	linm	ature			Ma	ture		
Start of week	2	ঘ	Allimmatures	*0	Lact. 9	R+U\$	Preg. 9	All humpbacks
22/5				3				3 7
29/5	- 1			6		1		7
5/6	3	3	6	21		7		34
12/6	1	3	4	25		12		41
19/6	3	3	6	46		15	1	68
26/6	3	1	4	44		18	1	67
3/7	1	4	5	76		17	3	101
10/7	2	1	3	52		29	7	91
17/7	1	1	2	63		35	-3	103
24/7		2	2	37		27	8	74
31/7		1	1	17		16	6	40
7/8	1	4	5	15		13	3	36
14/8		1	1	9		14		24
21/8	3	7	10	10		31	1	52
38/8	3	i	4	19		18		41
4/9	2	4	6	26		26		58
11/9	10	6	16	25		13	1	55
18/9	4	3	7	30		8	1	46
25/9	4	3	7	19		1		27
2/10		1	1	21				22
9/10	1	3	4	17		2		23
16/10	2		2	16				18
Total	44	52	96	605		304	35	1040

	Imm	ature			Mai	ure		
Start of week	*0	53	All immatures	Q	Lact. 9	R+U 9	Preg. 9	All humpbacks
5/6		-		2		1		3
12/6	1		1	2		2		5
19/6	1		1	13		1		1.5
26/6	4		4	30		7		41
3/7	6	- 1	7	35		10		52
10/7	10	2	12	39	. 1	8		59
17/7	4		4	30		2		36
24/7	4	6	10	25		7		42
31/7	2	2	4	36		12		52
7/8	5	-1	6	27		9		42
14/8	1	4	5	14		12		31
21/8	1		1	10		9		20
28/8	2	3	- 5	19		19		43
4/9	5	2	7	5		20		32
11/9	3	15	18	12		40		7()
18/9	5	4	9	12		37		58
25/9	6	9	- 15	21		20		56
2/10	5	4	9	58		17		84
9/10	2	1	3	44	1	16		6.3
16/10		2	2	24		3		29
23/10	2		2	29		5		37
30/10	_1_		1	8		1		10
Total	70	56	126	495		259		880

they were caught prior to mid-August. Among these, the order of appearance was the same as in post-war years, but the differences in mean dates were larger and were very highly significant. During the three weeks from mid-May into early June. immature animals only were caught. The mean date for immature whales (July 6) was 8 days earlier than for mature males, and two weeks earlier than for mixed females, but there are no data on which to subdivide the latter into lactating, resting and pregnant.

There are bimodal fluctuations within the post-war catches of southbound humpbacks (i.e., after mid-August) (Table 4, Figs 7-8) that cannot be explained by the writer. However, the pre-war catch sample from Durban in 1934 and 1935 was unimodal, and showed that immature whales precede mature males and mixed females on the southward migration.

Byron Bay, EA 29°S, Norfolk Island, 29°S, Moreton Island, EA 27°S. Catch samples from stations of eastern Australia and Norfolk Island have shared substantial similarities due to quotas and selection factors in common. The samples used for analysis include the following seasons and catches:- Byron Bay 1954-1961, 1040; Norfolk Island 1956-1961, 880; Moreton Island 1952-1961, 6205. Although variations in the size of catch at each locality tend to mask some of the similarities (Figs 9, 11, 13), the changes in percentage composition per fortnight at each are strikingly similar (Figs 10, 12, 14).

At each locality, the quotas during most of the seasons considered in this study were markedly smaller than the number of humpbacks sighted. This has made it possible for gunners to select more stringently than occurs at localities where there is only a small excess of sightings compared to eatch.

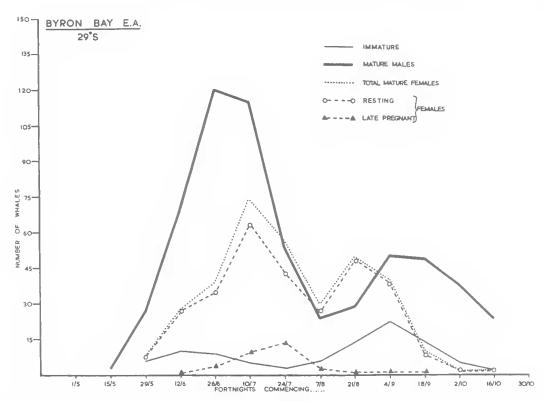


FIG. 9. Fortnightly catches of specified humpback categories, 1954-1961. Byron Bay, E Australia, 29°S.

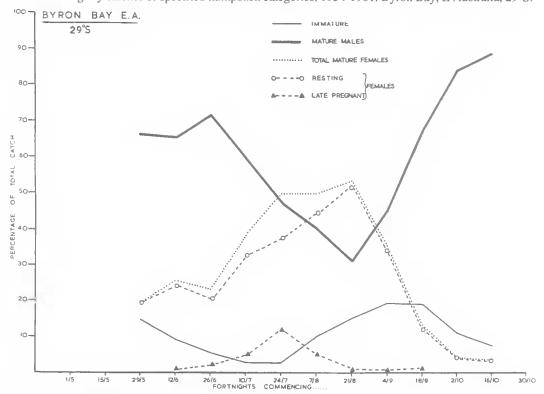


FIG. 10. Fortnightly percentages of specified humpback categories, 1954-1961, Byron Bay, E Australia, 29°S.

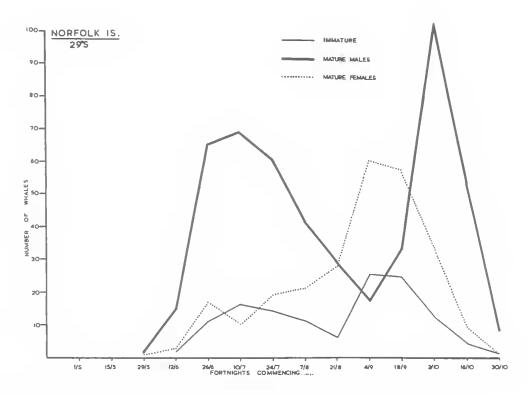


FIG. 11. Fortnightly catches of specified humpback categories, 1956-1961. Norfolk Is., 29°S.

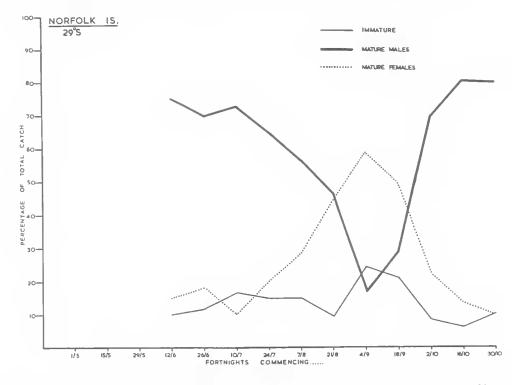


FIG. 12. Fortnightly percentages of specified humpback categories, 1956-1961. Norfolk Is., 29°S.

TABLE 7. W	eekly catches	of specified	humpbacks,
1952-1961. N			

	Imm	ature			Ma	ture		
Start of week	to	04	All immatures	ю	Lacr, 9	R+U 9	Preg. 9	All humpbacks
15/5				2				2
22/5				16		3		19
29/5	1	5	6	24		6		36
5/6	14	5	19	131		38	2	190
12/6	30	30	60	336		95		491
19/6	40	41	81	354		102	3	540
26/6	41	31	72	408		118	3	601
3/7	30	26	56	423		121	4	604
10/7	30	24	54	408		105	9	576
17/7	21	26	47	412		114	23	601
24/7	18	24	42	344		119	38	543
31/7	14	36	50	285		161	33	529
7/8	14	35	49	142		106	- 11	308
14/8	16	19	35	62		76	4	177
21/8	29	31	60	83		45	R	196
28/8	21	29	50	81		43	- 1	175
4/9	18	25	43	99		37		179
11/9	12	20	32	87		29	- (149
18/9	15	8	23	44		8		75
25/9	11	14	25	65		12	1	103
2/10	6	5	-11	57		3		71
9/10	2	2	4	10		4		18
16/10	1		1	13		2		16
23/10				6				6
Total	384	436	820	3892		1347	146	6205

From each station, it has been the practice to avoid adults accompanied by yearlings, whether or not the adults may have been females which were at the point of weaning offspring capable of independent existence. Late lactating females have therefore been largely absent from eatch samples.

Selection for size has been intense, especially during the early part of each season when gunners are usually hopeful of fulfilling the quota from large whales only. From each station, the whales caught during the earliest one or two weeks of the season have all been mature. Among the total catch of northbound humpbacks, the percentage of immature animals caught has been about one quarter of that at non-quota localities in the southern hemisphere (6, 12 & 11 for the former, 25-50 for the latter).

Since there is some indication that the underrepresentation of immature animals changes within each season according to the whalers' assessment of progress in filling the quotas, the available catch data may be a misleading sample of the local time sequence for immature whales. The calculated mean dates at each locality (Fig. 23, Table 12) show no significant differences from those of mature males. The latter are consistently earlier than mixed mature females which, due to selection against late lactating females, are mainly 'resting' animals.

Pregnant lemales are unrepresented in catches from Norfolk Island, but at Byron Bay and Moreton Island they form the last northbound category. The mean dates are approximately two weeks later than those for mature males at both localities.

Humpbacks classified as southbound have ineluded those caught after August 21 at Byron Bay and Moreton Island, and after September 4 at Norfolk Island, since equal proportions of northbound and southbound whales were sighted at the respective localities on these dates.

Mixed females (early pregnant and resting) form the earliest southbound category at each locality, but the differences in time in relation to immature whales is non-significant, except at Byron Bay (Fig. 25, Table 14), Mature males are later than immature whales by amounts which are highly significant in each locality (Moreton Is., 5 days; Byron Bay, 8 days; Norfolk Is., 14 days), Females in early lactation are unrepresented in catches, but Chittleborough (1962) has shown that this category is the last to travel south along the coast of eastern Australia.

Carnarvon, WA 25°S, Point Cloates, WA 22°S, At both these stations the quotas per season were larger than those for Byron Bay, Moreton Island and Norl'olk Island. The catch samples to be discussed here include Carnarvon 1950-1958, 5889, and Point Cloates 1949-1955, 3321. Catch ing at the latter locality ceased after the 1955 season. The length frequencies of catches indicates that gunner selection was usually less intense than at the latter stations and the catch samples used (1950-1958 at Carnaryon and 1949-1955 at Point Cloates) appear to be representative of the northbound population, except for humpbacks under 35 feet in length (Figs 15-18, Tables) 8-9). The sample classified as northbound includes all those caught before August 28 at Carnarvon and August 21 at Point Cloates (Chittleborough, 1953).

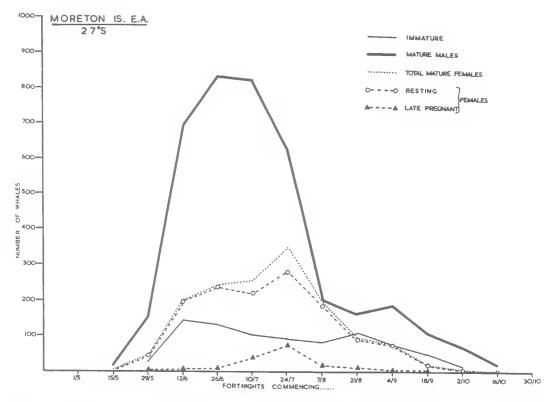


FIG. 13. Fortnightly catches of specified humpback categories, 1952-1961. Moreton Is., E Australia, 27°S.

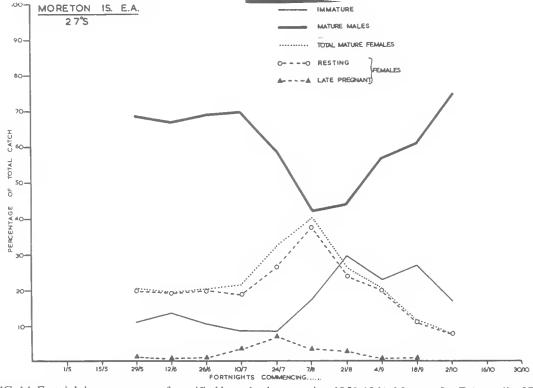


FIG. 14. Fortnightly percentages of specified humpback categories, 1952-1961. Moreton Is., E Australia, 27°S.

TABLE 8. Weekly catches of specified humpbacks, 1950-1958. Carnarvon, WA, 25°S.

Immature Mature 0+ 0+ All humpbacks immatures R + UStart of week O4 Preg. Lact ΑH 29/5 5/6 12/6 19/6 26/6 3/7 10/7 17/7 24/7 31/7 7/8 14/8 21/8 n 28/8 4/9 11/9 18/9 25/9 2/10 9/10 16/10 23/10 30/10 n Total

The number of females at the end of lactation have been calculated from mammary gland data kindly provided by Dr R.G. Chittleborough. Lactating females form the earliest category with mean dates (Fig. 23, Table 12) at Carnarvon 20 days and at Point Cloates 11 days prior to those for immature animals. The latter are 10 and 8 days earlier than the mean dates for mature males. The above time intervals are all very highly significant, but there is no significant difference between the mean dates for mature males and resting females.

Pregnant females form the last northbound group with mean dates 6 and 4 days later than mature males and about one month later than females at the end of lactation.

Catches off Western Australia during 1925-1928 were taken without quotas or length restrictions and therefore include a considerable number of the small size clases that are absent

TABLE 9. Weekly catches of specified humpbacks, 1949-1955. Point Cloates, WA, 22°S.

	Imm	ature			Ma	ture		
Start of week	10	20	Allimmatures	*0	Lact. 9	R+U \$	Preg. 9	All humpbacks
5/6	0	0	0	0	1	0	0	1
12/6	0	1	1	0	11	1	1	14
19/6	5	18	23	12	21	2	0	58
26/6	17	24	41	26	25	12	8	112
3/7	22	38	60	68	38	23	15	204
10/7	13	21	34	74	25	34	16	183
17/7	24	60	84	123	23	63	12	305
24/7	20	27	47	130	14	58	20	269
31/7	17	32	49	157	11	67	20	304
7/8	18	27	45	170	7	61	21	304
14/8	7	25	32	110	0	54	19	215
21/8	26	33	59	143	0	74	12	288
28/8	25	42	67	115	0	95	9	286
4/9	22	35	57	132	0	78	3	270
11/9	18	22	40	103	0	58	1	202
18/9	5	13	18	71	0	25	1	115
25/9	4	3	7	70	0	24	1	102
2/10	1	2	3	57	0	15	0	75
9/10	10.	0	0	12	0	2	0	14
Total	244	423	667	1573	176	746	159	3321

from post-war catches. Those of less than 30ft in length are of special interest, since they form the size classes represented among weaning 'yearlings'. In a total catch of 3,426 there were 174 examples occurring as follows:- 10 in June, 115 in July, and 49 in August. This represented 21%, 13% and 4% of the catch in these months and the 'yearlings' were clearly the earliest homogeneous group to pass the locality. Subsequent data have shown that most yearlings accompany the mother during the major part of the northward migration. Although the individual females cannot be specified from the data obtained during the above seasons, the time sequence of the yearlings is completely consistent with the occurrence of late lactating females as the earliest category in post-war catches. Immature animals (excluding yearlings) were the next group followed by mature males and mixed females. There are no data on pregnant animals. Thus all the categories which can be recognised in the 1925-1928 catches are consistent in time sequence with those in the 1949-1958 cathces.

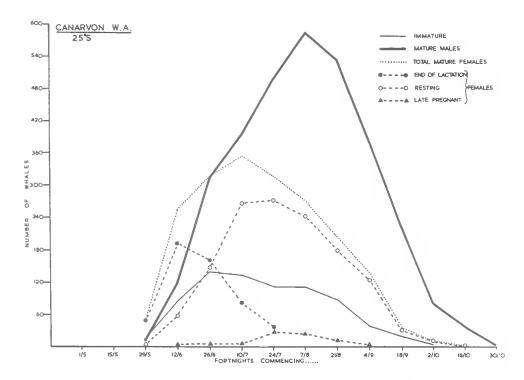


FIG. 15. Fortnightly catches of specified humpback categories, 1950-1958. Carnarvon, WA, 25°S.

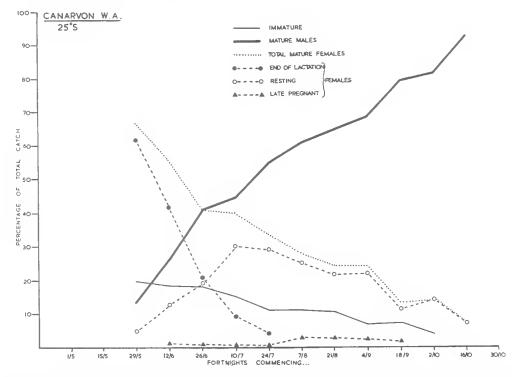


FIG. 16. Fortnightly percentages of specified humpback categories, 1950-1958. Carnarvon, WA, 25°S.

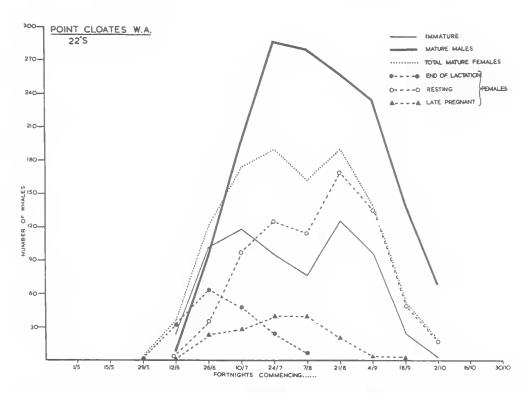


FIG. 17. Fortnightly catches of specified humpback categories, 1949-1955. Point Cloates, WA, 22°S.

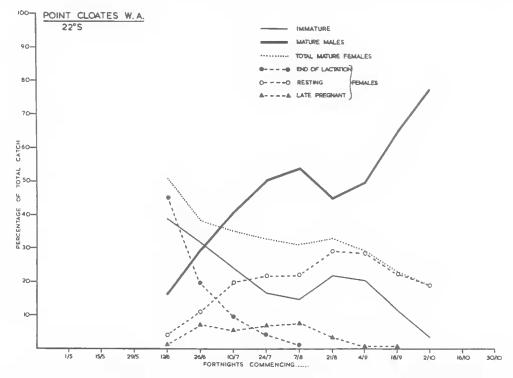


FIG. 18. Fortnightly percentages of specified humpback categories, 1949-1955, Point Cloates, WA, 22°S.

During the southward migration, immature animals have been the earliest recognisable category to travel past Western Australian land stations, while aerial observations by Chittleborough (1953) have shown that cows accompanied by young calves comprise the last group.

Madagascar, Pelagic, 16°-26°S. The catches from the coastal waters of Madagascar have been made by catchers operating with a factory ship that moved between 26°S & 16°S with 22°S as modal position. Irregularities of movement through this distance may have had some effects on catch composition, but there are no data indicating selection apart from rejection of undersized whales. There are no data on which to specify lactating females. The catch in 1948 and 1949 totalled 2014 humpbacks (Table 10, Figs 19-20) of which 1819 caught before September 11 have been classified as northbound. This date has been derived from descriptions of the above seasons by Angot (1951).

Immature animals form the earliest recognisable category to the extent that they occur in approximately equal numbers to those of mature males between mid-June and mid-July, but occur in smaller numbers than mature males during the remainder of the season. This results in a calculated mean date of July 28 (Table 12, Fig. 23) for immature animals compared with July 31 for mature males. While this interval of 3 days is small, it is nevertheless significant at the 1% level. Mixed females, including unspecified late lactating and resting animals show no significant difference in timing compared with mature males.

Pregnant females have a mean date 16 days later than mature males and are the last north-bound category.

The catches of southbound humpbacks (i.e., after September 11) were made during 3 to 4 weeks only. This period is insufficient to establish the time sequence of southbound animals passing Madagascar.

Congo, 1°S. There is little difference in latitude between Gabon and São Tomé Is, and the writer is unaware of significant differences in selection at the two localities. Catches have therefore been pooled under the heading 'Congo', and amount to 4,071 humpbacks taken during 1949 to 1952 (Figs 21-22, Table 11). As in the other post-war catches, animals under 35 feet in length are rarely represented. There are no data which can be used to specify animals that have been lactating re-

cently, so mature females include a mixture of the above and resting animals. Most females that were in late pregnancy when at higher latitudes have delivered their calves and became protected as cows accompanied by young calves before reaching 1°S. The catch of animals in late pregnancy has therefore been very small.

The Congo region is at or near the northern limit of the west African southern hemisphere humpbacks, so there is no clearly recognisable passage of northbound and southbound animals past the locality. Many specimens presumably remain for some weeks in the general breeding area before departing southwards, and there are no data on which to separate northbound from southbound animals. The total catch per season has therefore been used to calculate mean dates which, in these cases, represent the approximate mid-point between the beginning of northbound arrivals and the end of southbound departures for each category. This gives an earlier date for animals in late pregnancy relative to other categories since the former includes only northbound animals.

Immature animals form the earliest category (Figs 21-23) with the mean date on July 29 as compared with August 11 for mature males and mixed females (Table 12). Females in late pregnancy occur 10 days later on mean dates, and form the last category despite the non-representation of their southbound equivalents, (i.e., cows accompanied by young calves).

Tonga, 22°S. Unlike catches from all the preceding localities, those from Tonga have been taken predominantly from southbound animals, (Fig. 24, Table 13). The local whalers still use open boats, hand harpoons and hand lances, and with this equipment they concentrate, like many nineteenth century whalers with similar gear, on cows accompanied by young calves. This category is protected elsewhere by International Whaling regulations, and is unrepresented in other catches. While the catch from Tonga is small (82 in 5 years) it is nevertheless of special interest.

Hunting commences when cows with calves are first sighted, and these, together with immature whales up to about 38 fcet, comprise the subsequent catch. However, observations at Foveaux Strait, NZ, and along both west and east coasts of Australia indicate that cows and calves form the last southbound group.

The delay in hunting until cows and calves appear makes it highly probable that early southbound immature whales will be unrepresented in the catch. Nevertheless, the immature whales

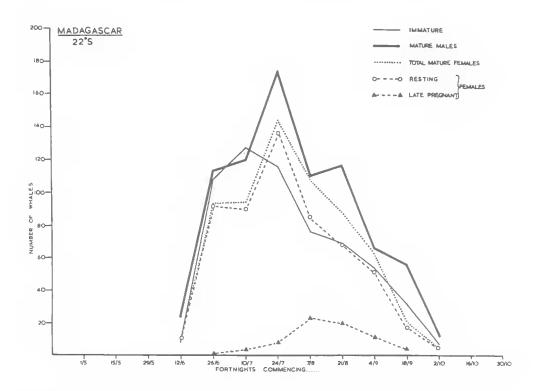


FIG. 19. Fortnightly catches of specified humpback categories, 1948-1949. Madagascar, 22°S.

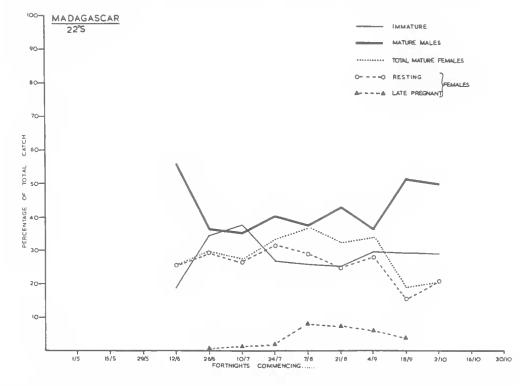


FIG. 20. Fortnightly percentages of specified humpback categories, 1948-1949. Madagascar, 22°S.

TABLE 10. Weekly catches of specified humpbacks, 1948-1949. Madagascar, pelagic, 16°S-26°S.

Immature Mature humpbacks mmatures R+D of week Preg. Lact. Start A All 12/6 19/6 26/6 3/7 10/7 17/7 24/7 31/7 7/8 14/8 21/8 28/8 4/9 11/9 18/9 25/9 2/10 .20 9/10 Total

caught during operations for cows and calves have a calculated mean date of August 29, which is 16 days earlier than for cows and calves. If allowance is to be made for immature whales that precede cows and calves, then the above difference in time would have to be increased. Table 13 shows that (except for one animal) cows and calves have been caught for approximately one month longer than immature humpbacks.

ANTARCTIC WATERS. It has been shown elsewhere (Dawbin, 1966) that the composition of the post-war catch samples show no significant difference between those caught in late December and those in early February. Pre-war samples in the 1932-1933 to 1938-1939 seasons included 13,357 catches between early November and late March. These were distributed between the south Atlantic Ocean and the eastern portion of the South Indian Ocean. This area includes regions with substantial differences in sea temperatures at equivalent latitudes and dates.

On the hypothesis that humpbacks would enter Antarctic sectors with warmest water earlier than sectors with colder water, a separation of the data

TABLE 11. Weekly catches of specified humpbacks, 1949-1952. Congo, 1°S.

	Imm	ature			Ma	ture		
Start of week	ď	0+	All immatures	ъ	Lact. 9	R+U \$	Preg. 9	All humpbacks
5/6	0	-1	1	0		1	0	2
12/6	9	13	22	21		19	1	63
19/6	16	21	37	39		34	1	111
26/6	39	48	87	73		46	0	206
3/7	42	37	79	117		81	0	277
10/7	45	54	99	139		77	0	315
17/7	54	56	110	153		85	2	350
24/7	55	50	105	157		101	3	366
31/7	52	54	106	167		93	3	369
7/8	37	47	84	143		103	3	333
14/8	32	42	74	123		77	4	273
21/8	29	37	66	136		93	10	310
28/8	18	17	35	121		79	7	242
4/9	18	16	34	121		81	4	240
11/9	10	10	20	105		65	1	191
18/9	3	10	13	103		56	4	176
25/9	6	4	10	53		46	1	110
2/10	2	3	5	51		27	0	8.3
9/10	2	-1	3	23		14	1	41
16/10	0	1	1	2		5	0	0
Tota1	469	522	991	1847		1188	45	407

into sectors of 20° longitude was made. Only two of these (20°E to 39°E and 80°E to 99°E) contained samples adequate for analysis. However, in the former sector cold water extends further north than in the latter at the same dates. Table 19 shows that by using mean dates as an index, humpbacks occur about three weeks later than in the latter sector.

Within each sector one would expect changes in local catch composition during the period that each category of humpbacks arrives or departs from Antarctic waters. In view of the consistently slow rate of humpback migration through a wide range of latitudes (Dawbin, 1966) and the relatively consistent difference in time sequence between categories in temperate and tropical waters as described previously, it seemed probable that time sequence changes would occur first at more northerly latitudes, e.g., 55°S and would be more or less duplicated at a later date in higher latitudes, e.g., 60°S or 66°S. To test this hypothesis the catch samples within sectors were subdivided into three degree lines of latitude. In the absence

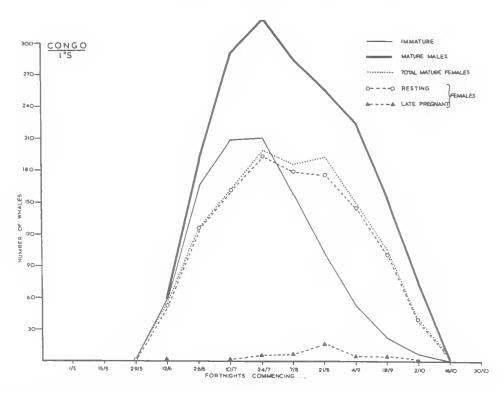


FIG. 21. Fortnightly catches of specified humpback categories, 1949-1952. Congo, 1°S.

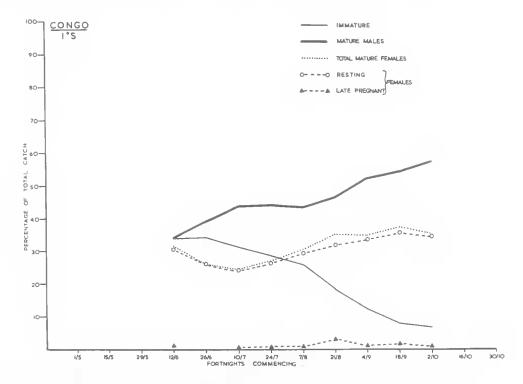


FIG. 22. Fortnightly percentages of specified humpback categories, 1949-1952. Congo, 1°S.

TABLE 12. Estimated mean date with standard deviation and the 95% confidence limits of the mean for specified categories of northbound humpbacks. * Since mixed females form a heterogeneous group, these data are not strictly comparable with those relating to the more homogeneous categories.

	Mean date	Week code mean	SD (n)	Confidence limits
Cook Strail, N2	2, 41°S			
Lact. 2	June 6	5.84	1.81 (120)	0.33
Immature	June 14	6.94	2.32 (620)	0.19
Mature &	June 29	9.00	2.53 (802)	0.18
Resting 7	July I	9.32	2.74 (216)	0.37
Preg. Q	July 8	10.34	2.21 (164)	0.35
All	June 24	8.29	2.76 (1922)	0.13
Great Barrier Is	NZ. 36°S			
Immature	June 19	7,63	1.70 (73)	0.40
Mixéd ♀ R+U	June 25	8.56 *	2.42 (41) *	0.76*
Mature &	June 30	9.27	2.27 (106)	0,44
Preg. 9	July 8	10.36	1.41 (11)	0.85
All	June 26	8.68	2,24 (231)	0.29
Albany, WA. 3	5°S			
Lact. 9	June 28	8.93	2,26 (69)	0.54
Immature	July 6	9.98	251 (164)	0.25
Mature &	July 16	11.50	2.42 (289)	0.28
Resting 🗣	July 20	12.10	2.34 (112)	0.44
Preg. ♀	July 30	13.52	1.87 (65)	0.46
All	July 14	11.17	2.64 (699)	0.20
Durban, Natal,	30°S			
Immature	July 7	10:23	2.52 (332)	0.27
Mature d	July 9	10.46	2.11 (212)	0.29
Mixed ♀ R+U	July 12	10.88 *	2.50 (123)*	().47*
All	July 8	10.42	2.40 (667)	0.19
Byron Bay, E	Australia, 29	S		
Immature	July 4	9,90	3.10 (39)	1.00
Manure d	July 8	10,35	2.51 (414)	0.25
Mixed P R+U	July 15	11.35 *	2.64 (204)*	0.37 *
Preg. 2	July 22	12.28	1.80 (32)	0.64
All	July 10	10.75	2.63 (689)	0.20
Norfolk Is., 29				
Mature of	July 23	12.44	2.86 (282)	0.34
Immature	July 25	12.73	2.76 (60)	0.72
Mixed ♀ R+U	Aug. 2	13.98 *	3.30 (99)*	0.66 *
All	July 25	12.83	3,01 (441)	0.28

of recognisilbe trends within this grouping, the data were pooled into two main groups of six degree lines including 55°S-60°S and 61°S-66°S (both inclusive) within each sector.

A few humpbacks only were caught within these sectors and latitudes duiring the 1932-1933 and 1933-1934 seasons, so these were eliminated in an attempt to reduce error due to seasonal variation. After these steps, the remaining samples between 55°S and 66°S included 5030 humpbacks in the sectors between 20°S to 39°S

	Mean date	Week code mean	SD (n)	Confidence limits
Moreton Is., E	Australia 276	S		
Mature o	July 9	10.48	2.62 (3347)	0.09
Immature	July 11	10.72	2.96 (571)	0,25
Mixed ♀ R+U	July 15	11.30 *	2.91 (1164)*	0:17 *
Preg. 9	July 25	12.76	1.78 (135)	0.31
All	July 11	10.75	2.75 (5217)	80.0
Carnaryon, WA	1, 25°S			
Lact, 🎗	June 28	8.97	2.09 (523	0.18
Immature	July 18	11.83	3.10 (636)	0.25
Resting ♀	July 26	12.90	2.60 (1087)	0.15
Mature 3	July 28	13.20	2.81 (2209)	0.12
Preg. 2	Aug 3	14.03	2.98 (68)	0.72
All	July 23	12.46	3.05 (4523)	0.09
Point Cloates,	WA, 22.5°S			
Lact. 9	July 9	10.50	2.10 (176)	0,31
Immature	July 20	12.08	2.30 (416)	0.23
Mature 3	July 28	13.22	2.02 (870)	0.13
Resting ♀	July 28	13:23	1.98 (375)	0.20
Preg. 9	Aug 1	13.80	2.83 (159)	0.38
All	July 25	12.79	2,32 (1996)	0.10
Madagascar, 1	6°S- 29°S			
Impature	July 28	13.20	2.95 (529)	0,25
Mixed 9 R+U	July 30	13.56	3.04 (521)	0.27
Mature &	July 31	13.69	3.14 (705)	0.24
Preg. 2	Aug 16	15.95	2.10 (64)	0.52
All	July 31	13.59	3.06 (1819)	0.14
Congo, I ² S				
Immature	July 29	13.35	3.48 (991)	0.22
Mature 3	Aug I1	15.23	4.10 (1847)	0.19
Mixed 9 R+U	Aug 11	15:23	4.19 (1188)	0.24
Preg. 9	Aug 21	16.69	3.26 (45)	0.99
All	Aug 8	14.79	4.07 (4071)	0.18

and 3938 in the sector between 80°E and 99°E. The weekly catch results are shown in Tables 15-18, and the fortnightly numbers and percentage groupings in Figs 26-27.

The results appear to be so inconsistent, whether considered by the above sectors and latitude groupings, or a variety of subdivisions within these, that the writer is unable to suggest any general trend in the order of arrival and departure of different humpback categories. It is clear that in Antarctic waters humpbacks, in general, are caught earlier in the sector of warmer waters (80°E to 99°E) then in the colder water sector and earlier in low latitudes (55°S to 60°S) than in higher latitudes (see also Table 19). However,

Table 13.	Weekly	catches	of	specified	humpbacks,
	61. Tonga			•	•

	Imma	ature						
Start of week	ъ	0+	Allimmatures	ъ	Lact. 9	R+U 9	Preg. 9	All humpbacks
24/7			1					1
31/7			1		2			3
7/8			2		1			3
14/8			5		2			7
21/8			3		7			10
28/8			3		8			11
4/9		1 8	4		2			6
11/9			2		9			11
18/9			1		12			13
25/9			1		2			3
2/10			2		3			5
9/10					4			4
16/10					1			1
23/10			1		2			3
30/10								
6/11					1			1
Total			_26		56			82

even this finding may be more a description of the movement of factory ships in relation to the edge of the pack ice than a true indication of humpback movements.

If differences in actual mean dates for all humpbacks at each of the four regions are disregarded for the purposes of discussion, it is still clear from Figs 26-27 and Table 19, that there are very small and inconsistent differences in the relative timing of humpback categories within each region.

Based on mean dates, there is a maximum difference of nine days between the earliest and last of the four identifiable humpback categories. Even within this limited period, the apparent sequence on mean dates is different within each of the four groupings (Table 19). The catch composition also differs substantially in fortnightly frequency (Figs 26-27). If the catch is an adequate sample of the local humpback composition, then the above results indicate that movements of different humpback categories in Antarctic waters between late November and mid-March are mainly random.

There are several factors that may contribute to this negative result. In Antarctic waters, the movements of factory ships and chasers have been directed primarily towards catching fin and

TABLE 14. Estimated mean date with standard deviation and the 95% confidence limits of the mean for specified categories of southbound humpbacks.

	Mean date	Week code mean	SD (n)	Confidence limits
Tonga, 22°S				
Immature	Aug 29	17.78	3.36 (28)	1.27
Lact. ♀	Sept 14	20.04	3.01 (56)	0.80
All	Sept 9	19.29	3.29 (84)	0.72
Moreton Is., E	Australia, 27	°S		
Mixed ♀ R+U	Sept 6	18.96	1.83 (183)	0.27
Immature	Sept 8	19.21	1.95 (249)	0.25
Mature ਹੈ	Sept 13	19.96	2.22 (545)	0.18
All	Sept 11	19.58	2.13 (977)	0.13
Byron Bay, E	Australia, 29°	S		
Mixed ♀ R+U	Sept 4	18.69	1.70 (100)	0.58
Immature	Sept 14	20.11	2.20 (57)	0.45
Mature of	Sept 22	21.22	2.47 (191)	0.35
All	Sept 16	20.31	2.48 (348)	0.27
Norfolk Is., 29	°S			
Mixed ♀ R+U	Sept 24	21.44	1.86 (160)	0.30
Immature	Sept 24	21.52	1.86 (66)	0.46
Mature ♂	Oct 8	23.52	1.86 (213)	0.25
All	Oct 1	22.46	2.12 (439)	0.20
Great Barrier Is	., NZ, 36°S			
Immature	Oct 7	23.39	2.36 (13)	1.41
Mixed ♀ R+U	Oct 8	23.47	2.17 (15)	1.18
Mature ♂	Oct 24	25.80	0.50(5)	0.59
All	Oct 17	23.79	2,22 (33)	0.77

blue whales with humpbacks as a rather secondary objective. In coastal areas such as the offshore waters from Durban, it has already been argued that such selection might significantly affect catch composition. However, there is no substantial evidence to show that such differential selection will invalidate humpback sampling on the open seas distant from shore lines.

As a more simple hypothesis, I suggest that the catch sample has been taken after a large proportion of the humpbacks had already reached Antarctic waters, and that sampling ended before any significant emigration from the region had commenced.

The season during which southbound hump-backs pass many tropical and temperate localities is known, and at an overall migration rate of 15° per month (Dawbin, 1966), it can be shown that in most sectors more than half of all humpbacks could be expected south of 55°S by late November. If the sequence followed in warmer waters is still maintained during progress into high latitudes, then all main categories of humpbacks

should already be represented south of 55°S before December, with the possible exception of cows accompanied by calves. Cows accompanied by calves receive full protection, and therefore do not contribute to the catch. The absence of samples during much of the period of entry into high latitudes would contribute greatly to a masking of trends.

The period of emigration from Antarctic waters as calculated from the time of appearance of northbound humpbacks at lower latitudes, indicates that very few animals are likely to pass north of 55°S until late April, i.e., after catch sampling in high latitudes has ceased. Similar calculations for 60°S and other high latitudes are consistent with the view that the catch sampling in Antarctic waters during 1934-1939 occurred during months in which entry and exit of humpbacks was too small to become evident.

Catches were made during considerably longer seasons in the Falkland Island Dependencies region 1910 to 1917. Data from these catches have been examined, but they include such wide differences between individual companies operating in proximity to each other that the writer has failed to establish consistent trends.

It should be noted that these early records were made at a time when many whales were dismembered alongside anchored factory ships, thus adding difficulties in obtaining accurate length measurements, and complicating any examination for foetuses. Inspectors concerned primarily with eatch examination were not required by International regulations until 1937.

CONCLUSIONS

Northbound humpbacks have been sampled by catches between 41°S and 1°S and include mate-

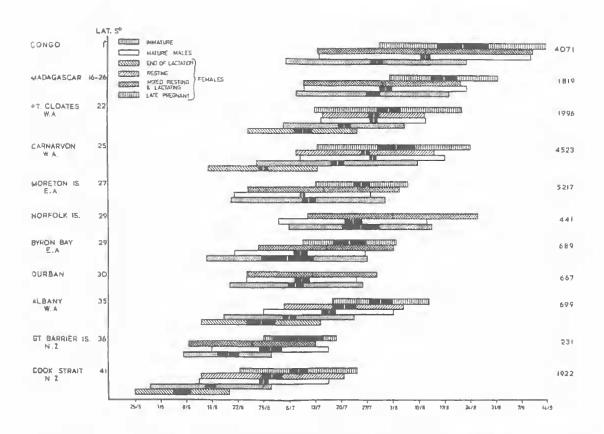


FIG. 23. The period of passage of specified northbound humpbacks as shown by catch composition in temperate and tropical waters. Mean date for each category shown as vertical white line. 95% confidence limits for the mean shown in black. One standard deviation either side of the mean shaded.

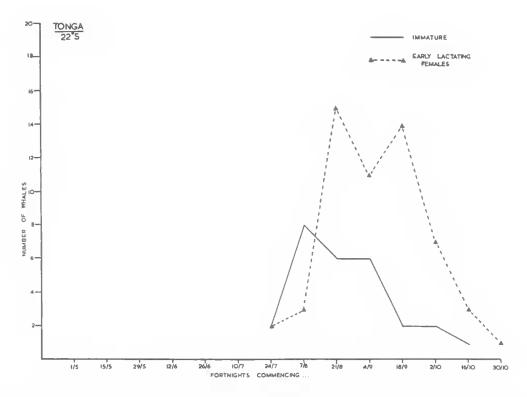


FIG. 24. Fortnightly catches of southbound immature humpbacks and lactating females, 1957-1961. Tonga, 22°S.

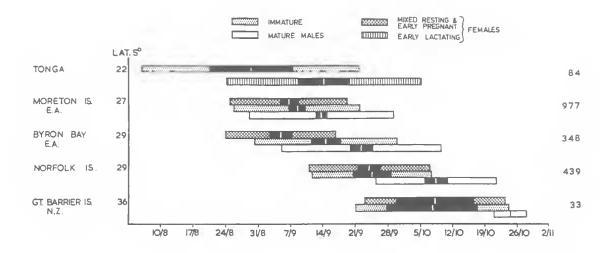


FIG. 25. The period of passage of specified southbound humpbacks as shown by catch composition in temperate and tropical waters. Mean date for each category shown as vertical white line. 95% confidence limits for the mean shown in black. One standard deviation either side of the mean shaded.

TABLE 15. Weekly catches of specified humpbacks, 1934/35 to 1937/38. Longitudes 20°E-39°E, latitudes 55°S-60°S.

Immature Mature All humpbacks All immatures R + Uweek Preg. 0+ of Start 6/11 13/11 20/11 27/11 4/12 11/12 18/12 25/12 1/1 8/1 15/1 22/1 29/1 5/2 12/2 19/2 26/2 5/3 12/9 Total

rial relating to at least four segregated breeding stocks. These stocks include one or more groups that pass between east Australia and Tonga, one along west Australia, another past Madagascar and another along West Africa to the Congo. Despite the sampling differences between localities as described in the text, catches from all these stocks share similarities in the time sequence followed by specified categories of humpbacks (Fig. 23, Table 12).

Females at the end of lactation and still accompanied by weaning 'yearlings' occur earliest at all localities from which the data allow identification of this group. At Cook Strait, Albany, Carnarvon and Point Cloates, they occur at an average of 12 days earlier than immature whales. There is no regular difference in timing between immature males and immature females. Mature males follow immature whales at Cook Strait, Great Barrier Island, Albany, Durban, Carnarvon, Point Cloates, Madagascar and Congo by an average of 8 days later. As described previously, there is no significant difference in timing between these categories at the three stations where quotas and

TABLE 16. Weekly catches of specified humpbacks, 1934/35 to 1937/38. Longitudes 20°E-39°E, latitudes 61°S-66°S.

	Imma	ature			Mature		
Start of weck	60	0+	All immatures	60	R+U 9	Preg. 9	All humpbacks
4/12		1	1	3			4
11/12		1	1				1
18/12	1		1				1
25/12	1	1	2	1	9	1	13
1/1	1	9	10	6	11	3	30
8/1	2	3	5	7	9	4	25
15/1	1	2	3	9	12	7	31
22/1	6	5	11	25	37	12	85
29/1	9	10	19	26	19	15	79
5/2	29	37	66	119	93	30	308
12/2	20	32	52	60	65	26	203
19/2	40	41	81	124	66	28	299
26/2	5	6	11	28	8	6	53
5/3	10	8	18	28	15	5	66
12/3	5	2	7	13	12	2	34
19/3	5	4	9	4	1		14
26/3				62	19	_12	102
Total	135	162	297	515	376	151	1348

intense selection for large animals has resulted in marked under-representation of immature animals (Byron Bay, Norfolk Island, Moreton Is-

TABLE 17. Weekly catches of specified humpbacks, 1934/35 to 1937/38. Longitudes 80°E-99°E, latitudes 55°S-60°S.

	Imma	ature		Mature			
Start of week	@ 20	0+	All immatures	*◊	R+U \$	Preg. 9	All humpbacks
16/11	2	3	5	3	10	16	34
13/11				1	6	18	25
20/11	8	7	15	16	49	28	108
27/11	5	23	28	21	84	13	146
4/12	26	31	57	104	138	50	344
11/12	19	32	51	100	85	49	285
18/12	21	32	53	132	146	56	387
25/12	4	12	16	55	64	51	186
1/1	4	9	13	30	45	33	121
8/1	4	18	22	43	45	9	119
Total	93	167	260	505	667	323	1755

TABLE 18. Weekly catches of specified humpbacks, 1934/35 to 1937/38. Longitudes 80°E-99°E, latitudes 61°S-66°S.

Immature Mature All humpbacks mmatures \Box 50 04 50 Preg. 02 Start of Alli 27/11 1 7 4/12 3 3 9 11/12 6 2 9 21 18/12 12 20 32 17 23 108 36 25/12 16 17 33 59 53 23 168 1/1 12 23 35 114 38 18 8/1 25 55 42 204 17 42 65 28 15/1 33 61 64 53 39 217 22/1 41 57 98 100 72 42 312 29/1 20 35 55 33 231 78 65 5/2 28 29 57 23 241 100 61 12/2 28 25 53 84 95 246 1.4 19/2 34 40 74 62 54 12 202 26/2 13 11 24 21 21 q 75 5/3 5 9 8 35 4 13 Total 253 316 569 713 587 314 2183

land). However, there is no case in which mature males have preceded immature whales by an amount that is significant at the 5% level.

Mature females that are predominantly in the resting condition have occurred at an average of only 3 days after mature males so can be regarded as following a similar time sequence to the latter. The apparent timing of mixed females is variable due to the unknown but certainly different proportions of late lactating and resting animals included in this group at different localities. For this reason it is not strictly comparable with the more accurately specified categories. In general, mixed females have a mean date which falls after those for immature whales and before those for pregnant females. Pregnant females have been represented at all localities except Norfolk Island and Durban. In all cases where they are represented, they occur as the last northbound category. The average intervals are 11 days after mature males, 19 days after immature animals and 31 days after lactating females.

Due to sampling errors discussed previously, the above time intervals are not regarded as having the precision implied by expressing the results in days, but the results should be a reasonable indication of the order of time difference between categories. For the reasons given previously, it is

TABLE 19. Estimated mean date with standard deviation and the 95% confidence limits of the mean for specified categories of Antarctic humpbacks.

	Mean date	Week code mean	SD (n)	Confidence limits
80°-99°E, 55°-	60°S			
Preg. ♀	Dec 13	5.94	2.33 (323)	0.26
Non-preg. 9	Dec 14	0.16	2.04 (667)	0.16
Immature	Dec 14	6.11	1.98 (260)	0.26
Mature of	Dec 18	6.58	1.76 (505)	
All	Dec 15	6.21	2.02 (1755)	0.16
80°-99°E, 61°-	66°S			
Preg. 9	Jan 19	11.23	2.92 (314)	0.33
Mature ♂	Jan 27	12.33	2.84 (713)	0.21
Immature	Jan 27	12.34	2.94 (569)	0.25
Non-preg. ♀	Jan 28	12.51	2.81 (589)	0.23
All	Jan 28	12.22	2.90 (2185)	0.12
20°-39°E, 55°-	60°S			
Non-preg. 9	Jan 2	8.77	3.17 (1049)	0.20
Immature	Jan 4	0.16	3.33 (954)	0.22
Mature of	Jan 5	9.25	3.01 (1403)	0.16
Preg. 2	Jan 11	10.13	3.24 (276)	0.39
All	Jan 4	9.14	3.18 (3682)	0.16
20°-39°E, 61°-	-66°S			
Nen-preg. ♀	Feb 11	14.55	2.74 (376)	0.26
Preg. ♀	Feb 13	14.77	2.73 (151)	0.45
Immature	Feb 14	14.88	2.49 (297)	0.29
Mature d	Feb 19	15.62	2.85 (515)	0.25
All	Feb 15	15.06	2.76 (1339)	0.15

probable that the differences described here are minimal and likely to be greater in the migrating population than shown by catch samples.

Southbound humpbacks form a smaller and more complex sample which has been discussed at greater length elsewhere (Dawbin, 1966). Based on mean dates, mixed females together with immature animals, form the earliest southbound categories (Fig. 25, Table 14). In these cases, mixed females include those in very early pregnancy unseparated from resting females. Many of these females would correspond to those that travelled north early when at the end of lactation. If these females also returned south early, then many would be incorrectly included amongst the northbound whales which overlap with southbound up to the time that 50% are sighted travelling north and 50% travelling south. This, combined with a lack of data on which to separate early pregnant from resting females impedes attempts to estimate a mean time interval for these females (see also Dawbin, 1966), but they clearly precede mature males and cows with

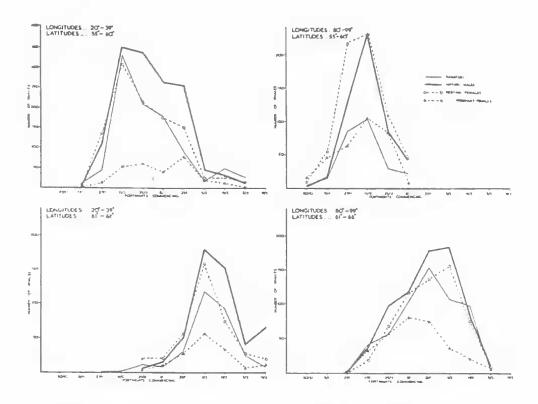


FIG. 26. Fortnightly catches of specified humpback categories, Antarctic, 1934/35 to 1938/39 seasons. Longitudes 20°E to 39°E and 80°E to 99°E, latitudes 55°S to 60°S and 61°S to 66°S for each longitude group.

calves and the data are not inconsistent with the view that many may precede immature hump-backs.

Immature humpbacks travel south about 10 days earlier than mature males and the latter in turn precede cows accompanied by young calves. Subtraction of the 10 days' difference between immature animals and mature males as above, from the 16 days' difference between immature animals and cows with calves at Tonga appears to indicate a difference of 6 days only (figure used by Dawbin, 1966) between mature males and cows with calves. However, reasons for believing that the ealculated interval at Tonga is an underestimate have been discussed previously. In addition, the observations of Chittleborough near Point Cloates 22°S (1953) and Bryon Bay 28°S (1962) together with those of the writer in Foveaux Strait 48°S, have shown that eows accompanied by ealves comprise considerably more than 50% of all humpbacks at these latitudes during the final three or four weeks of the southward migration past each locality. Thus any nonlactating females and late immature animals together with mature males, are considerably outnumbered by cows and calves at this stage. The latter, which comprise the females that travelled north last as pregnant animals, are clearly the last category to return south. The available data on the time sequence of southbound humpbacks is not inconsistent with the view that humpbacks return south in approximately the same sequence as they follow during the migration north.

Antarctic catch samples, when subdivided according to latitudes and sectors of longitude, indicate differing time sequences between samples. There is, therefore, no consistent trend recognisable in the present analysis of Antarctic catches. Since most of the samples were obtained after late November, it seems probable that they were obtained from a population that had already stabilised considerably as a result of the arrival of most catchable categories into the Antarctic sampling zone. This hypothesis is consistent with the expected arrival dates based on known mean dates in lower latitudes and a migration rate of

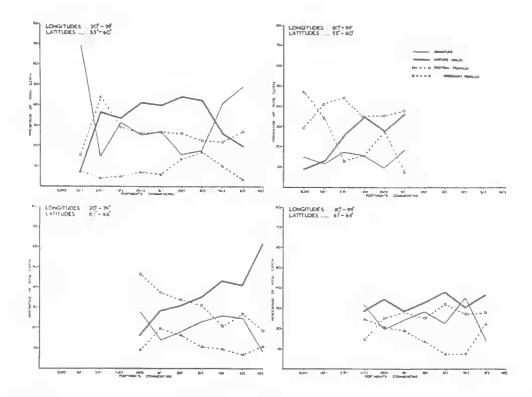


FIG. 27. Fortnightly percentages of specified humpback categories, antarctic, 1934/35 to 1938/39 seasons. Longitudes 20°E to 39°E and 80°E to 99°E, latitudes 55°S to 60°S and 61°S to 66°S for each longitude group.

about 15° per month. On the same evidence, no consistent changes in composition would be expected before the northward departure of some humpbacks in mid to late April, i.e., considerably later than the period during which eatch sampling occurred. In the absence of consistent trends in Antarctic samples, the order in which the specified humpback categories travel past each locality and the time intervals between the earliest and each of the later categories have been estimated exclusively from temperate and tropical data.

The estimated humpback sequences differ markedly from those of fin whales described by Laws (1961) who discusses extensive Antarctic data and the findings of previous workers, especially Mackintosh (1942). Laws concludes that both the north and south migrations of older fin whales and of pregnant females are in advance of those of other groups, and that sexually immature animals are later. Pregnant humpbacks appear to travel south in advance of other humpbacks, but return north after other categories. Immature

humpbacks are the second group in both south and north migrations, followed by mature males together with resting females, while lactating females travel south last and return north in advance of other humpbacks.

There is no consistent evidence that different humpback categories either migrate at different speeds or stay for significantly different lengths of time in the breeding areas. The data indicate that most categories depart also from the feeding areas in the same order as they arrive. Most categories therefore spend more or less equal periods in Antarctic waters. The main exception are breeding females which, when pregnant, spend a prolonged period in the feeding regions and, when lactating, spend an abridged period, while resting females stay for approximately the same length of time as mature males and immature humpbacks.

The implications of these findings in relation to the breeding cycle and the environmental conditions encountered during migration are discussed more fully elsewhere (Dawbin, 1966).

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